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Carbon isotope ratios of plants of a tropical dry forest in Mexico

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Abstract. Carbon isotope ratios were measured on leaves of the dominant species within a tropical dry forest in Mexico, which was characterized as being strongly drought deciduous. A variety of succulent epiphytes from diverse microsites had carbon isotope ratios indicating obligate crassulacean acid metabolism. All woody species examined had isotope ratios indicative of the C₃ photosynthetic pathway, although there was a wide range of isotopic values. Two of the woody species that retained leaves during the dry season showed a large variation in carbon isotope ratios (up to 6‰) that was dependent on microsite location.

Key-words: Epiphytes, isotope ratios, crassulacean acid metabolism, water-use-efficiency, succulents

Introduction

Carbon isotope ratios ($\delta^{13}\text{C}$) at natural abundance levels have frequently been used as a means for determining the photosynthetic pathway used by a species. C₄ photosynthetic pathway plants have $\delta^{13}\text{C}$ values in the range of -9 to -14‰ as do drought-adapted succulent plants with obligate crassulacean acid metabolism (CAM); facultative CAM plants have carbon isotope ratios between -14 and -20‰ (Mooney, Troughton & Berry, 1974; Troughton, 1979). C₃ plants typically have carbon isotope ratios between -22 and -32‰ (Troughton, 1979). More recently, Farquhar, O'Leary & Berry (1982b) have extended our understanding of carbon isotope ratios in plants and have developed a model which indicates that leaf carbon isotope ratios in C₃ plants are a reliable long-term measure of intercellular carbon dioxide

levels. There is now substantial evidence in support of this model from a broad diversity of species (Farquhar *et al.*, 1982a; Farquhar & Richards, 1984; Ehleringer *et al.*, 1985; Seemann & Critchley, 1985; Farquhar *et al.*, 1988).

As an ecological application of this model, carbon isotope ratios provide an indication of plant water-use-efficiency for C₃ species. This follows because under steady state conditions, photosynthesis (A) and transpiration (E) are both dependent on leaf conductance (g):

$$E = \Delta w \cdot g \quad \text{Equation 1}$$

$$A = (c_a - c_i) \cdot g / 1.6 \quad \text{Equation 2}$$

where c_a is the ambient carbon dioxide concentration (assumed to be $340 \mu\text{l l}^{-1}$), c_i is the intercellular carbon dioxide concentration, Δw is the leaf to air water vapour concentration gradient and 1.6 is the ratio of the diffusion coefficients of water to carbon dioxide in air.

Since stomata govern the rates at which carbon dioxide and water vapour diffuse into and out of a leaf, the relative differences in water-use-efficiency (ratio of photosynthesis to transpiration, A/E) of different species or of plants within different microhabitats can be calculated from

$$A/E = (c_a - c_i) / (1.6 \cdot \Delta w) \quad \text{Equation 3}$$

A fraction of the carbon fixed will be lost through respiration (θ), and therefore we expect the long-term water-use-efficiency (W), often referred to also as the transpiration efficiency, to be

$$W = (1 - \theta) \cdot (c_a - c_i) / (1.6 \cdot \Delta w) \quad \text{Equation 4}$$

In many ecological or community-level comparisons, it is reasonable as a first approximation to assume that leaf temperatures and therefore Δw values are similar among species. Therefore, with long-term estimates of c_i obtained by carbon isotope ratio analysis, we also have a direct relative measure of long-term leaf water-use-efficiency.

$\delta^{13}\text{C}$ values reflect not only the water economy of individual plants but also, when values are viewed collectively for a local flora, the aridity of a given locality (Mooney, Troughton & Berry, 1974; Smith, Griffiths & Lüttge, 1986; Eickmeier &

Bender, 1976; Winter & Troughton, 1978; Ehleringer & Cooper, 1988). For example, a photosynthetic pathway shift occurs in Trinidad from predominantly C₃ epiphytic bromeliads at high rainfall regimes (>2.5 m annually) to predominantly CAM epiphytes in lower rainfall regions (Smith, Griffiths & Lüttge, 1986). On a more subtle scale, Ehleringer & Cooper (1988) have shown that $\delta^{13}\text{C}$ in C₃ desert plants at both the single-species and community levels increased as soil moisture levels decreased.

In this study, we have (1) examined the photosynthetic pathway types of dominant species within a seasonally dry tropical rain forest site in western Mexico and (2) correlated patterns of C₃ water-use-efficiency to habitat and life form.

Materials and methods

We examined 51 species from the flora of a tropical dry forest in western Mexico (Lott, 1985; Lott, Bullock & Solis Magallanes, 1987). This site, the Estacion de Biologia Chamela of the Universidad Nacional Autonoma de Mexico, is located on the Pacific coast in the state of Jalisco (10°30'N, 105°03'W). Mean annual rainfall is 748 mm and falls principally between the months of July and October (Bullock, 1986). The dominant growth form of the vegetation is a drought deciduous tree. However, the vegetation is also rich in both epiphytes and vines.

Leaf material from all of the succulents were collected during the dry season (March), as were leaves of two tree species that produce new leaves early in the dry season ('dry-season green'), *Forchhammeria* and *Jacquinia*. The former is deciduous for a brief period at the end of the wet season; *Jacquinia* is leafless throughout the wet season. Leaves of the tree species that produce leaves early in the wet season ('wet-season green') were collected in October.

Samples of epiphytic succulents were collected from different portions in the forest canopy as were samples of tissue of columnar emergent cacti. Some ground-dwelling succulents, as indicated in the results, were collected from both understory and fully exposed habitats. Leaves of individuals of some of the wet-season green trees were collected from a mesic site in a canyon bottom, whereas others of the same species were collected from ridge tops.

Long-term estimates of the intercellular carbon dioxide concentration (c_i) were calculated by

rearranging the equations originally developed by Farquhar *et al.* (1982b) as

$$c_i = c_a \cdot ([\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{leaf}}] / [b - a] - a / [b - a]) \quad \text{Equation 5}$$

where $\delta^{13}\text{C}_{\text{air}}$ and $\delta^{13}\text{C}_{\text{leaf}}$ are the carbon isotope ratios of the air (-7.8‰) and leaf, respectively, a is the discrimination associated with the slower diffusion rate of ¹³CO₂ ($a = 4.4\%$) and b is the net discrimination against ¹³CO₂ associated with RuBP carboxylase ($b = 27$).

Carbon isotope ratios were determined on bulked samples. The sample was dried, ground to 40 mesh and then sub-sampled. Carbon isotope ratios were determined on carbon dioxide collected from combusted samples using a Finnigan MAT delta E isotope ratio mass spectrometer. Carbon isotope ratios are expressed relative to the PDB standard using the equation:

$$\delta^{13}\text{C} = (R_{\text{sample}} / R_{\text{standard}} - 1) \cdot 1000 \quad \text{Equation 6}$$

where $\delta^{13}\text{C}$ is the carbon isotope ratio of the sample in parts per ml (‰), R_{sample} and R_{standard} are the ¹³C/¹²C ratios of sample and standard, respectively. The precision of each isotopic measurement is 0.02‰ and repeatability of each sample was ±0.08‰.

Results and discussion

All of the succulent bromeliads, orchids, agaves and cacti species at Chamela had carbon isotope values indicating they were obligate CAM ($\leq -15\%$) (Table 1). In contrast, the succulent vines, trees and shrubs, which in total represented 18 families, were all C₃. Calculated intercellular CO₂ values in C₃ plants were highest in wet-season green trees, intermediate in dry-season green trees and lowest in the evergreen-leaved trees. Water-use-efficiencies would follow the opposite pattern, with the evergreen-leaved plants having the highest water-use-efficiencies. There were no C₄ perennials.

The effect of microhabitat on carbon isotope ratios for CAM plants was examined under both lower versus upper canopy positions and sun versus shade conditions. No differences were noted in the carbon isotope ratios of epiphytes growing on lower stems versus the upper canopy (~6 m) of trees, nor in tissues from the base as contrasted with the top of emergent cacti (~5 m) (Table 2). Additionally, leaf carbon isotope ratios of CAM plants did not change between sun and shade habitats (Table 3). In a similar situation,

Medina & Minchin (1980) had noted differences in the leaf carbon isotope ratios of C₃ epiphytes and supporting trees with canopy position in a tropical forest in Venezuela. They assumed that these differences in carbon isotope ratio arose primarily because of source differences in the atmosphere CO₂ (lower canopy CO₂ being heavier in ¹³C because of decomposition processes). Ehleringer *et al.* (1985) and Francey *et al.* (1985) provided data suggesting that changes in carbon isotope ratio with canopy position were more likely the result of changes in leaf intercellular CO₂ levels. Data from CAM plants at the Chamela site, which is substantially drier and more open than the tropical forests studied by Medina & Minchin (1980), are supportive of the notion that leaf δ¹³C

values are determined primarily by physiological processes and that any potential CO₂ source effects on leaf isotope values are small.

Leaf carbon isotope ratios of the C₃ woody plants were dependent on microsite position. Plants from dry ridge top sites averaged higher carbon isotope ratios by 1–6‰ than plants from mesic arroyos (Table 4). Of these species, the dry-season green trees (*Forchhammeria* and *Jacquinia*) had substantially higher δ¹³C values at the dry site, indicating a higher water-use-efficiency. Ehleringer & Cooper (1988) had noted a similar pattern with Sonoran Desert shrubs, with δ¹³C values increasing by 2–4‰ in going from relatively wetter wash sites to the drier slopes.

The carbon isotope ratios of the succulent

Table 1. Leaf δ¹³C isotope ratios (‰) of plant species at Chamela, Mexico. Authorities for taxonomy are given by Lott (1985).

Growth form	Range	Sample size
I. Succulents		
A. Bromeliaceae		
<i>Aechmea bracteata</i>	–15.4	1
<i>Billbergia mexicana</i>	–14.1 to –15.3	3
<i>Bromelia palmeri</i>	–12.7 to –13.2	2
<i>B. plumieri</i>	–12.9 to –15.1	3
<i>Hechtia</i> sp.	–13.8 to –14.4	2
<i>Tillandsia circinnata</i>	–11.6 to –13.0	4
<i>Tillandsia diguetii</i>	–14.2	1
<i>Tillandsia fasciculata</i>	–12.0 to –14.2	4
<i>Tillandsia ionantha</i>	–11.5 to –14.7	6
<i>Tillandsia makoyana</i>	–10.4 to –15.3	11
<i>Tillandsia setacea</i>	–10.9 to –11.4	2
<i>Tillandsia usneoides</i>	–13.9	1
B. Orchidaceae		
<i>Erycina echinata</i>	–11.9	1
<i>Campylocentrum</i> sp.	–11.4 to –14.4	3
<i>Myrmecophila chinodora</i>	–11.2 to –12.2	2
<i>Oncidium</i> sp.	–14.8	1
C. Agavaceae		
<i>Agave angustifolia</i>	–12.2 to –13.1	3
<i>Agave colimana</i>	–13.6	2
D. Cactaceae		
<i>Acanthocereus occidentalis</i>	–13.1 to –13.2	3
<i>Cephalocereus purpusii</i>	–11.7 to –13.7	3
<i>Mammillaria</i> sp.	–12.2	1
<i>Nopalea karwinksiana</i>	–11.9 to –14.0	2
<i>Opuntia excelsa</i>	–12.5 to –13.7	8
<i>Opuntia puberula</i>	–11.9 to –12.9	8
<i>Pachycereus pecten-aboriginum</i>	–11.5 to –13.0	3
<i>Peniocereus cuixmalensis</i>	–13.3 to –14.9	4
<i>Peniocereus rosei</i>	–12.3	1
<i>Selenicereus vagans</i>	–13.0	1
<i>Stenocereus chrysocarpus</i>	–13.3 to –15.5	3
E. Vines		
<i>Cissus sicyoides</i>	–24.7 to –26.5	2
<i>Philodendron warscewiczii</i>	–24.3 to –27.6	6

Growth form		Range	Sample size
II. Trees and shrubs*			
<i>Acacia angustissima</i>	w	-26.9	1
<i>Apoplanesia paniculata</i>	w	-27.3	1
<i>Bursera instabilis</i>	w	-26.8	1
<i>Caesalpinia coriaria</i>	w	-26.9	1
<i>Caesalpinia sclerocarpa</i>	w	-26.5	1
<i>Capparis indica</i>	w	-26.4 to -28.6	7
<i>Capsicum annuum</i>	w	-28.7	1
<i>Casearia corymbosa</i>	w	-28.1	1
<i>Chlorophora tinctoria</i>	w	-26.7	1
<i>Citharexylum</i> sp.	w	-24.8	1
<i>Coccoloba liebmannii</i>	d	-24.8 to -28.8	5
<i>Colubrina triflora</i>	w	-27.6	1
<i>Cordia alliodora</i>	w	-27.0 to -30.0	6
<i>Croton pseudoniveus</i>	w	-27.3 to -28.8	6
<i>Erythroxylum havanense</i>	w	-27.0	1
<i>Forchhammeria pallida</i>	e	-21.9 to -26.2	3
<i>Hamelia versicolor</i>	w	-27.4	1
<i>Jacquinia pungens</i>	d	-22.4 to -28.9	8
<i>Stemmadenia</i> sp.	w	-28.8	1
<i>Thevetia ovata</i>	w	-27.6	1
III. Summary			
A. Succulents			
Vines		-24.3 to -27.6	2
Orchids		-11.2 to -14.8	4
Bromeliads		-10.4 to -15.4	12
Cactus		-11.5 to -15.5	11
Agaves		-12.2 to -13.1	2
B. Trees and shrubs			
Wet season green		-24.8 to -30.0	17
Dry season green		-22.4 to -28.9	2
Evergreen		-21.9 to -26.2	1

*w = wet season green tree or shrub, d = dry season green tree or shrub and e = evergreen tree or shrub.

Table 2. Leaf $\delta^{13}\text{C}$ isotope ratios (‰) of epiphytic and non-epiphytic CAM species occurring in different canopy positions at Chamela, Mexico.

	Lower canopy	Upper canopy
Non-epiphytic		
<i>Opuntia excelsa</i>	-12.8, -13.0	-12.5, -13.3
<i>Pachycereus pecten-aboriginum</i>	-11.5	-13.0
Epiphytic		
<i>Tillandsia circinnata</i>	-11.6	-11.9, -12.8
<i>Tillandsia makoyana</i>	-12.6	-12.1, -12.6

Table 3. Leaf carbon isotope ratios (‰) of CAM plants in sun and shade microsites at Chamela, Mexico.

	Shade	Sun
<i>Bromelia plumieri</i>	-14.6, -15.1	-12.9
<i>Opuntia puberula</i>	-12.4, -12.5, -12.9	-12.9
<i>Stenocereus chrysocarpus</i>	-13.5	-12.3

Table 4. Leaf carbon isotope ratios (‰) of C₃ species in microhabitats differing in soil moisture availability at Chamela, Mexico. Data are means ± 1 SD.

		Arroyo	Ridge
<i>Capparis indica</i>	w*	-28.4 ± 0.2	-27.2 ± 0.7
<i>Cordia alliodora</i>	w*	-29.6 ± 0.7	-27.7 ± 0.9
<i>Croton pseudoniveus</i>	w*	-28.1 ± 0.6	-27.9 ± 0.8
<i>Forchhammeria pallida</i>	e*	-25.3, -26.2	-21.9
<i>Jacquinia pungens</i>	d*		
October		-26.3 ± 1.0	-24.2 ± 0.5
March		-28.9	-22.4

*w = wet season green tree or shrub, d = dry season green tree or shrub and e = evergreen tree or shrub.

bromeliads of Chamela can be contrasted with those of Trinidad. At Trinidad both C₃ and CAM bromeliads occur. At rainfall amounts below 2000 mm only CAM species are found (Smith *et al.*, 1986). At Chamela, where rainfall has not reached 1000 mm in at least 10 yr, all of the bromeliads were CAM. Smith *et al.* (1986) found little variation in the carbon isotope ratio of a given species of bromeliad within Trinidad. Similarly, at Chamela little variation was found in the isotope ratios of epiphytic bromeliads (*Tillandsia* spp.) by microsite, although there was perhaps some minor microsite variation in the ground-dwelling *Bromelia plumieri* (E. Morren) L. B. Smith. It is of note though that of the few species in common between Chamela and Trinidad, those of Chamela had higher carbon isotope ratios. Smith *et al.* (1986) report $-18.6 \pm 0.8\%$ for *Bromelia plumieri*. At Chamela, values for this same species ranged from -12.9 to -15.1% . *Tillandsia usneoides* (L.) L. at Trinidad is reported at -19.8% ; we measured a value for Chamela plants of -13.9% . *Tillandsia fasciculata* Sw. was reported by Smith *et al.* to be -14.1% at Trinidad. At Chamela, values of -12.0 to -14.2% were measured.

It appears that those species dependent on atmospheric water sources at Chamela are less affected by microsite than those depending on soil moisture. These epiphytes operate with obligate CAM photosynthesis and do not appear to utilize C₃ photosynthesis for carbon gain even during the rainy season. The most striking variation found was among the dry-season green trees (*Forchhammeria* and *Jacquinia*). When growing at dry microsites, these species evidently restrict their stomatal conductance to a sufficient degree that intercellular CO₂ levels are reduced by as much as $90 \mu\text{l l}^{-1}$ between wet and dry seasons. The observed carbon isotope ratio difference of up to -6% between wet and dry site plants is greater than that

found by Farquhar *et al.* (1982b) for two mangrove species grown under a wide range of salinity conditions, by Ehleringer *et al.* (1986) for plants growing under different irradiance conditions, or by Ehleringer & Cooper (1988) for desert plants growing under contrasting soil moisture availability.

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References

- Bullock, S.H. (1986) Climate of Chamela, Jalisco and trends in the south coastal region of Mexico. *Archives for Meteorology, Geophysics and Bioclimatology, Series B*, **36**, 297–316.
- Ehleringer, J.R. & Cooper, T.A. (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia*, **76**, 562–566.
- Ehleringer, J.R., Field, C.B., Lin, Z.F. & Kuo, C.Y. (1986) Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. *Oecologia*, **70**, 520–526.
- Ehleringer, J., Schulze, E.-D., Ziegler, H., Lange, O. L., Farquhar, G. D. & Cowan, I. R. (1985) Xylem-tapping mistletoes: water or nutrient parasites? *Science*, **227**, 1479–1481.
- Eickmeier, W. G. & Bender, M.M. (1976) Carbon isotope ratios of Crassulacean acid metabolism species in relation to climate and phytosociology. *Oecologia*, **25**, 341–347.
- Farquhar, G.D. & Richards, R.A. (1984) Isotope composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology*, **11**, 539–552.
- Farquhar, G.D., Ball, M.C., van Caemmerer, S. & Roksandic, Z. (1982a) Effect of salinity and humidity on $\delta^{13}\text{C}$

- value of halophytes: evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO₂ under different environment conditions. *Oecologia*, **52**, 121–124.
- Farquhar, G.D., Hubick, K.T., Condon, A.G. & Richards, R.A. (1988) Carbon isotope fractionation and plant water-use efficiency. In *Stable Isotopes in Ecological Research* (ed. P.W. Rundel, J.R. Ehleringer & K.A. Nagy), (in press). Springer-Verlag, Berlin.
- Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982b) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121–137.
- Francey, R.J., Gifford, R.M., Sharkey, T.D. & Weir, B. (1985) Physiological influences on carbon isotope discrimination in huon pine (*Lagarostrobos franklinii*). *Oecologia*, **66**, 211–218.
- Lott, E.J. (1985) *Listados Florísticos de México*. III. La Estación de Biología Chamela, Jalisco. Herbario Nacional, Universidad Nacional Autónoma de México, México.
- Lott, E.J., Bullock, S.H. & Solis Magallanes, J.A. (1987) Floristic diversity and structure of upland and arroyo forests in coastal Jalisco, Mexico. *Biotropica*, **19**, 228–235.
- Medina, E. & Michin, P. (1980) Stratification of $\delta^{13}\text{C}$ values of leaves in Amazonian rain forests. *Oecologia*, **45**, 377–378.
- Mooney, H.A., Troughton, J.A. & Berry, J.A. (1974) Arid climates and photosynthetic systems. *Carnegie Institution of Washington Year Book*, **73**, 793–805.
- Seemann, J.R. & Critchley, C. (1985) Effects of salt stress on the growth, ion content, stomatal behavior, and photosynthetic capacity of a salt-sensitive species, *Phaseolus vulgaris* L. *Planta*, **164**, 151–162.
- Smith, J.A.C., Griffiths, H. & Lüttge, U. (1986) Comparative ecophysiology of CAM and C₃ bromeliads. I. The ecology of the Bromeliaceae in Trinidad. *Plant, Cell and Environment*, **9**, 359–376.
- Troughton, J.H. (1979) $\delta^{13}\text{C}$ as an indicator of carboxylation reactions. In *Encyclopedia of Plant Physiology*, New Series, Vol. 6. Photosynthesis II, Photosynthetic Carbon Metabolism and Related Processes (ed. M. Gibbs & E. Latzko), pp. 140–149. Springer Verlag, Berlin.
- Winter, K. & Troughton, J.H. (1978) Photosynthetic pathways in plants of coastal and inland habitats of Israel and the Sinai. *Flora*, **167**, 1–34.

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